V. *Notes on Flower-Haunting Diptera.* By George Francis Scott-Elliot, M.A., B.Sc., F.L.S., etc., communicated by Herbert Goss, F.L.S.

[Read February 19th, 1896.]

I have recently been engaged in writing a Flora of Dumfriesshire, and on beginning, it seemed to me advisable to make a new departure in several respects from the plan usually followed in such works, which is practically that of the late Mr. Hewett C. Watson drawn up in 1851. Amongst other points I have thought it necessary to observe insect visitors, and for this reason. The entire dependence of most flowers on their insect *clientèle* for fertilisation has been proved over and over again, and therefore it follows that to understand the distribution of species in any small area, it is necessary to know the insects which visit the species in that area. Moreover there are many theories at present abroad as to the origin of variations by natural causes, and as most botanical characters depend on those parts of the flower which are adapted to insects, the importance of a knowledge of these latter can scarcely be overrated.

Besides their importance in this respect, as being a possibly direct agency in the origin of variations in plants, insects must play an enormous indirect part in the isolation of flowers. If flowers of the same species are growing partly inside a sheltered and shady wood and partly on the bare ground outside that wood, it seems to me, from my own observations, that they will most certainly not be visited by the *same* insects. It is not improbable that a Bombus or hive bee, or possibly a butterfly, will visit both the forms outside the wood and those within it; but I do not think I am at all rash in saying that probably not 5 per cent. of those outside will be fertilised by pollen from those inside the wood, and *vice versa*. This means, for reproduction, nearly perfect *isolation*, and, therefore, just as we find in the case of oceanic islands, the formation of new varieties may proceed indefinitely.

I must, however, state at once that I have no pretensions to be an entomologist, and that in the determination of the insects I have not attempted any naming on my own part, but have trusted entirely to the kindness and skill of Mr. R. Service and Mr. E. Brunetti. The flowers, whose visitors have been caught by myself or my friends the Misses Hannay and Taylor and Mr. Armstrong, are nearly 300 in number, and in the work alluded to, the insects are put in their proper place after the locality of each species.* I found, however, as I proceeded with the catching of insect visitors, several very great difficulties. One is the want of any handy book of English Diptera by which one could tell the particular group of Diptera at a glance when in the field. I do not see why such a book should not be very easily produced by some of the members of the Entomological Society. About five plates ought to enable one to tell at once the group (*Asilidæ, Bombylidæ, Conopidæ, Dolichopidæ, Empidæ, Leptidæ, Muscidæ, Stratiomyidæ, Syrphidæ*, etc.; there are twenty groups or families given in Müller's "Fertilisation of Plants," p. 641. The number of species given in this work is 253, so that a short account and clavis of each genus and of the species in *e.g., Syrphidæ* and *Bombylidæ* would not make a book of more than a hundred pages.

The next difficulty was insuperable. It is not possible to be at the side of every flower in the flora for every hour in the day, during the whole time that it is in bloom, for obvious reasons. I question if it is possible to do in a thorough manner, more than six species in a season. Hence the visitors of these 300 flowers are simply the usual common forms.

The first interesting point which I noticed with regard to both Diptera and Hymenoptera was that they are extraordinarily quick to see even the slightest motion. By remaining perfectly still one can observe the shyest Syrphid at work, but a very slight gesture of the hand is sufficient to send it off like a flash, and unless one remains very still there is no chance of getting the majority of visitors.

The next point, which can only be proved by observa-

* A list of insects with the flowers which they visit is placed at the end of this paper.

tion, remembering the foregoing hint, is mentioned chiefly in order, if possible, to get some information from those present at this Meeting. I have come to the conclusion that the majority of Diptera have a recognized space up and down which they are continually flying. I have frequently had to remain as quiet as possible for three hours beside some interesting flower, and on these occasions I have seen the same fly perpetually flying up and down within perhaps 10 or 15 yards, occasionally stopping to rest and then resuming its patrol. For the carrion flies the phenomenon is very easy to observe, and I fancy that the whole country is really marked out into beats for each individual or pair. If a piece of carrion or excrement is deposited on a particular spot, it is astonishing that it should be so soon covered by hundreds of *Lucilia Cæsar*, *Scatophaga*, etc. In fact, I have a strong suspicion that these creatures divide the ground in the way that vultures do in tropical countries, and that when the first one detects the smell, the difference in his flight or his absence from his proper place tells that in the next beat, and so on; the knowledge is thus conveyed with astonishing rapidity from beat to beat, and crowds continue to flock in until the first comers are satisfied and fly back to their places. I mention this as the result of observation, though not by an entomologist, and chiefly with a view to extracting information. The importance of it will be obvious with regard to the question of isolation already mentioned, for if every fly, or at any rate, most of the flower-haunting species usually remains or remain in the same small locality under ordinary conditions, it is obvious that there is practical isolation in very circumscribed habitats. The larval forms of Diptera and the plants on which they feed seem to be very little studied, and this is also of great importance to botanists, because I fancy that this has a great deal to do with the occurrence of flowers in great numbers at definite places. Thus on the bare wind-swept low-lying seashore, between the Annan and Kirtle, I found the Diptera very few in number and particularly limited in species. Such flies as *Lucilia*, *Anthomyia radicum* and *Chortophila*, appeared to fertilize most of the seaside plants. On the other side of the Solway, where there are cliffs, and these are interrupted by bays and many small burns, the abundance of

Diptera is extraordinary. I suspect the shelter afforded by these bays and valleys has much to do with this abundance.

Speaking generally, these flower-haunting Diptera appear to be far most frequent on plants which grow in enormous numbers wherever they do occur. Thus on *Spergula arvensis* I found *Syritta*, three species of *Platychirus*, *Rhingia*, *Empis vitripennis* and many *Anthomyia*, *Scatophaga*, etc. This was also the case on the common watercress, which is visited by *Volucella bombylans*, *Eristalis arbustorum*, *E. sepulchralis*, *Helophilus pendulus*, *Syritta pipiens*, *Platychirus clypeatus*, *P. peltatus*, *Empis livida*, and fourteen other Diptera and Coleoptera. On the more local and scattered *N. palustre* I only discovered three common Anthomyids.

Probably this explains why it is that so many plants have taken to contracting their inflorescence so that a very large number of flowers can be visited by insects in a very short time. Thus, of all the plants which I have studied, perhaps the following are the most visited by Diptera and other insects, viz., the dwarf elder, sheepsbit, *Umbelliferæ*, particularly *Cicuta* and *Angelica*, and of course the *Compositæ*, notably *Aster tripolium*.

On flowers which come early in the spring or late in the autumn, there is, in favourable weather, quite an extraordinary number of insects. I consider this to be probably due to the whole available insect force being concentrated on just those few forms which happen to be in bloom. The following list of visitors:—Hive bee, five species of *Bombus*, *Pieris napi*, *Eristalis pertinax*, *Sericomyia borealis*, *Platychirus albimanus*, *Syrphus balteatus*, *S. topiarius*, *Anthomyia radicum*,* would be at once supposed to belong to some very high type of flower, such as a *Labiate*, but in reality they were all caught on the common bramble or blackberry, which probably attracted them because the special bee-flowers were not then in bloom. Similarly the early spring buttercup or pilewort rejoices in a large number of guests, *e.g.*, Hive bee, *Mantua napi*, *Melanostoma*, *Platychirus albimanus*, *Empis punctata*, *E. bilineata*, *Hyetodesia basalis*, *Chilosia* sp., *Anthomyia* sp., and *Meligethes*.

* By the author, Miss Hannay, and Mr. J. C. Willis.

One point which comes out very clearly in many different cases is also illustrated by the buttercups. That is, that the water-loving forms of a genus, such as in this case *R. aquatilis* and *R. sceleratus,* are visited by perfectly extraordinary swarms of very low-class Diptera, while the guests of the land-forms though fewer in number, are of a much higher type (*e.g., R. ficaria,* v.s.). These water species of a genus are also usually botanically less specialised than their land allies,* so that the specialisation of the insects and of their hosts has advanced together.

This corresponding rise in the scale of specialisation of guests and host together comes out very clearly in a variety of genera, and is strongly in favour of the correctness of the general theory to which I shall allude later on. Thus *Geum urbanum* is yellow and of a simple open type, and is visited by *Siphona geniculata, Hydrotea dentipes, Anthomyia radicum,* and *Hylemyia strigosa.*

Geum rivale is red and of a very much more complicated type, and this is visited by *Bombus muscorum* and *hortorum,* as well as *Rhingia rostrata.*

Epilobium angustifolium has also a larger, more tubular and one-sided flower than the ordinary willow herb *E. montanum.* Hence one finds upon it the hive bee and bumbles as the most regular visitors. (*Apis, Bombus lucorum, B. pratorum, Vespa sylvestris,* and *Cyrtoneura stabularis*).

The other only received the visits of *Syritta pipiens, Platychirus clypeatus, Siphona cristata,* and *Anthomyia radicum.*

The cloudberry, *Rubus chamæmorus,* is also either degraded or an earlier form of *Rubus* than the common blackberry, and hence it is not surprising that only a species of *Empis,* which Mr. Brunetti thinks is new to Britain, *Anthomyia radicum, Siphona cristata,* and *Hydrotea dentipes* were discovered upon it. Two very curious instances of the effect of structure of flower on insect visitor may be mentioned in this connection. *Corydalis,* a kind of poppy, belonging to one of the earliest

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* *R. sceleratus* has small petals, conical axis, etc., and *R. aquatilis* is white, not yellow.

and least specialised orders, has a corolla closed like that of the peas, and its visitors are the regular pea-flower types, *Apis*, three species of *Bombus*, *Apathus*, and *Andrena*. The *Labiatæ* are, again, of all orders the most obviously adapted to bees, and the most constantly visited by them; for instance, of the fifteen flowers of this order observed by myself and friends, the visitors were invariably bumble bees and hive bees, except in one case,—*Mentha arvensis*,—where we found only *Scatophaga*, *Siphona*, *Hydrotea*, *Lophius*, and *Telephorus*. This flower is, again, a water-loving form, and also of very much simpler structure than any of the other plants of this order studied.

The flower-haunting Diptera are very much more important than most observers imagine in fertilisation. Thus such genera as *Galium*, *Myosotis*, some species of *Veronica*, and the smaller geraniums, particularly *G. lucidum*, appear to be chiefly dependent on *Syrphidæ* for setting seed. Now in Sir J. Lubbock's book, "Ants, Bees, and Wasps," these Diptera are somewhat markedly left out in the cold, so that a few facts, drawn from my experience, as to their colour, sense, and intelligence, may be of interest. I am obliged to admit that they are more frivolous than bees, and perhaps visit only three flowers in half an hour, during which time a *Bombus* might visit at least one hundred. On the other hand, they do not, as a rule, mix their honeys, but keep pretty steadily (though not so closely as a true bee) to one particular nectar. I have seen this particularly with *Empis vitripennis* when visiting *Linum catharticum*, which was growing along with many other flowers. It kept steadily to the *Linums* for a considerable time.

Their colour sense is quite clearly obvious from the following table. The most remarkable fact in it is, that not one of these sixteen Diptera is confined to yellow and white flowers. Sixty-one per cent. of the flowers visited by *Rhingia rostrata* are blue or red, and usually the white flowers visited are under 50 per cent. of the whole.

	Number of Flowers visited.	White Flowers.	Yellow Flowers.	Red Flowers.	Blue Flowers
		Per cent.	Per cent.	Per cent.	Per cent.
Empis bilineata . .	8	50	25	...	25
„ *livida* . . .	10	40	10	30	20
„ *vitripennis* . .	6	50	17	33	...
Eristalis arbustorum .	9	67	22	...	11
„ *pertinax* . .	14	64	22	14	...
Melanostoma mellinum	9	45	33	22	...
Morellia hortorum . .	9	29	29	29	13
Onesia sepulchralis .	6	33	33	33	...
Platychirus albimanus	25	40	24	12	24
„ *clypeatus*	25	20	36	20	24
„ *manicatus*	15	54	6	40	...
„ *peltatus* .	15	47	13	27	13
Rhingia rostrata . .	13	23	16	46	15
Syritta pipiens . . .	21	67	24	9	...
Syrphus cinctellus . .	7	58	14	14	14
„ *ribesii* . . .	19	48	37	10	5
HYMENOPTERA.					
Bombus muscorum .	45	11	18	49	22*
Andrena albicans . .	8	50	37	13	...
Allantus nothi . . .	18	53	26	16	5

It thus appears that, though *Bombus muscorum* is far more red-loving than the higher Diptera, this is by no means the case for the smaller bees. There are in fact only four of the sixteen Diptera quoted, which are fonder of white flowers than *Andrena albicans* and *Allantus nothi*. The fact that blue and purple flowers, which are held by Müller and others to be particularly adapted to bees, and almost entirely fertilised by them, are very frequently visited by these Diptera, is particularly important. *Empis bilineata, Platychirus albimanus* and

* Miller gives for flies 67·9 per cent. white and yellow flowers and 30·3 per cent. of red and blue; for higher bees 36·6 per cent. white and 63·3 per cent. red and blue, *cf.* 29 per cent. white and 71 per cent. red and blue in this table; for small bees 63·8 per cent. white and 36·2 per cent. red or blue; while here it is 83 per cent. white and 17 per cent. red. "Alpenblumen," 1881, p. 512.

clypeatus, are more blue in their tastes even than *Bombus muscorum*; and no less than ten of these sixteen Diptera habitually visit flowers of this colour. Very much the same deduction can be drawn with regard to their taste for red tints. *Platychirus manicatus* and *Rhingia* are nearly as fond of red as the *Bombus muscorum*, and only five out of these sixteen Diptera are less fond of red than *Andrena albicans* and *Allantus*.

If, in fact, we take the average colour-preferences of these sixteen Diptera, we find them to be as follows: Average of Diptera: 46 per cent. white; 22 per cent. yellow; 21 per cent. red; 10 per cent. blue; from which it clearly follows that these Diptera are of far more advantage to red and blue flowers than either *Andrena* or *Allantus*.

When, instead of taking colour in flowers as a base of classification, we look to complexity of structure; we find ourselves at once in a position of considerable difficulty. The structure of flowers cannot be easily brought into perfectly definite and unmistakable groups such as are furnished by the four colours already mentioned.

If we group flowers according to their natural orders, and tabulate insect visits to those orders, the result is quite meaningless, because plants belonging to the same order, or even genus, are in respect to insects of very different complexity. Thus, *Geranium sylvaticum*, *e.g.*, is visited by insects which bodily enter the open cup-like flower; while *Geranium lucidum* is visited by insects which stand on the petal and insert the proboscis into the narrow short tube. Hence I found on *Geranium sylvaticum*, *Apis*, *Bombus pratorum*, *B. muscorum*, *Halictus cylindricus*, *Nomada lateralis*, *Empis tessellata*, *E. pennata*, *E. vitripennis*, and sp., *Platychirus peltatus*, *P. manicatus*, and five *Anthomyidæ*, which could not be named. That is a very varied and extensive *clientèle*.

On *Geranium lucidum*, on the other hand, I only found *Syrphus cinctellus*, *Melanostoma mellinum*, *Platychirus manicatus* (though in great numbers); but no *Anthomyidæ* or Hymenoptera. This represents, of course, a very different set of visitors. The difference in *Leguminosæ* betwixt the small yellow trefoils and *Ornithopus* and the rest of the order is also most

remarkable, and similar differences occur in almost all orders and more than one genus. Müller tabulates several orders with their visitors, and his example has been followed in this country by Mr. J. C. Willis and others.

However, as a rough classification, in order to obtain some insight into the intelligence of these Diptera, I arranged all the flowers which I have examined into six divisions :—

1. *Ranunculus* group, including all open flowers rich in pollen, into which any insect may enter bodily.

2. *Crucifer* group, including such forms as *Umbelliferæ, Galium, Alisma,* as well as all *Compositæ* with extremely short florets, such as, *e.g.*, Daisy.

3. *Veronica, Myosotis,* etc., *i.e.*, flowers with a distinct though short tube, and which involve higher intelligence in their clients than the preceding.

4. The long-tubed *Compositæ* such as *Carduus,* and also *Lychnis,* etc.

5. The smaller *Leguminosæ, Medicago, Ornithopus,* and *Trifolium procumbens.*

6. The larger *Leguminosæ.*

To these six classes I have added *Ajuga* (or *Euphrasia*), *Scilla,* and *Orchis.*

The result is expressed on the next page :—

PERCENTAGES OF VISITS TO FLOWERS.

	Flowers visited.	Open. Class 1.	Crucifer. Class 2.	Veronica. Class 3.	Carduus. Class 4.	Medick. Class 5.	Ulex. Class 6.	Ajuga or Euphrasia.	Scilla.	Orchis.
Empis bilineata . . .	8	25	37	25	13	...	...	...	...	...
„ *livida*	10	10	30	10	40	...	10	...	...	...
„ *vitripennis* . .	6	34	34	...	16	...	...	...	...	16
Eristalis arbustorum .	9	...	89	11	...	...	...	...	...	...
„ *pertinax* . .	14	14	50	...	22	...	7	...	...	7
Melanostoma mellinum .	9	56	11	11	...	11	...	11	...	...
Morellia hortorum . .	9	...	33	...	67	...	...	...	...	...
Onesia sepulchralis . .	6	...	50	...	50	...	...	...	...	...
Platychirus albimanus .	25	20	44	24	...	4	...	4	4	...
„ *clypeatus* .	25	8	24	28	16	8	12	4	...	...
„ *manicatus* .	15	27	27	13	33	...	...	...	...	...
„ *peltatus* . .	15	27	27	20	13	...	...	13	...	...
Rhingia rostrata . . .	13	31	23	8	23	...	...	8	7	...
Syritta pipiens . . .	21	5	86	5	4	...	...	...	...	...
Syrphus cinctellus. . .	7	15	57	14	...	...	...	...	14	...
„ *ribesii* . . .	19	16	48	5	21	...	5	...	...	5*
Now, if this is compared with the same Hymenoptera, we find :—										
B. muscorum	45	20	2	5	22	...	27	24	...	...
Andrena albicans. . .	8	37	37	...	26	...	...	...	...	...
Allantus nothi . . .	18	11	55	11	11	...	6	6	...	...

* *Cf.* Müller, "Alpenblumen," Leipsig, 1881, p. 512.

In words this may be translated to mean that these Diptera are, on the whole, more intelligent than the lower class Hymenoptera.

Three species of Diptera visit species of Orchidaceæ. In fact, *Syrphus ribesii*, *Eristalis pertinax*, and *Empis vitripennis*, appear to be the main agents in effecting the fertilisation of our common British forms. The only other insect which I have myself as yet discovered on these plants is *Argynnis aglaia*; my friend, Mr. Armstrong, however, reports that he has observed certain "large brown and sulphur moths" feeding on *Habenaria bifolia*.*

Nine of these Diptera are found either on the larger *Leguminosæ*, flowers of the Bugle type, or on Orchids; and this is sufficient to show a very considerable amount of intelligence.

It is not easy to bring these insects into any series which will show their relative ability, but judging from the preceding table, the following is a pretty sound grading of their intelligence:—

Class 1. *Bombus.*

„ 2. *Empis vitripennis, Eristalis pertinax, Syrphus ribesii.*

„ 3. *Empis livida, Melanostoma, Platychirus albimanus, P. clypeatus, P. peltatus, Rhingia, Allantus.*

„ 4. Remainder, including *Andrena albicans.*

It remains to point out the bearing of the foregoing remarks on the use of Diptera and other insect visitors.

I have not found any confirmation of certain theories which suggest that the actual probing of an insect's proboscis, or the friction of its feet have any influence in determining the growth of hairs, or the flow of sugar to that particular part of the flower;† it is, of course, probable that the continual draining away of nectar from a certain spot will induce a larger supply to come to that particular position, just as the continual use of a certain muscle will produce a greater enlargement of it. It is even probable that such a demand for nectar may be inherited, but this is not yet proved.

* I have taken specimens of *Leucania turca* in the New Forest with the pollinia of this species attached to their heads.—H. G.

† The researches of M. Kustenmacher on Galls, Bot. Gaz., xx., p. 497, are, so far as hairs are concerned, rather against this view, which is not, to my knowledge, supported by any direct evidence.

On the other hand, I am far more certain of the dependence of flowers on insects than I was before. When such minute forms as *Draba verna*, *Subularia aquatica*, or such "typical wind-fertilised" species as the Burnet, Salad Burnet, and Dog's Mercury, and species of such genera as *Thalictrum* and *Plantago* are found to be visited by insects, as I have myself seen in the course of my work, it leads one to doubt if wind-fertilisation is ever of much use. A simple mathematical proof shows that the chances of a piece of pollen from one flower reaching that of another growing within a foot of it, is about one to three hundred; but if an insect is on one flower, for any purpose, the chance that it will go to the next visible flower is probably ten to one.

It seems to me that these Diptera will probably yield the most valuable results in investigating the origin of plant species, for they visit all kinds of flowers, and possess both colour-sense and intelligence, as I have tried to show. In fact, it is to them that we probably owe all the neatly made, small and bright-coloured forms which are particularly abundant in this country. It is not possible now to say definitely, that this or that insect is responsible for such a flower (though I think, myself, I could say it for certain forms); a genus in which seven species have been studied by us, and on which we have found hive bees and bumbles in all cases except two, would imply a very high botanical structure. Yet this genus is *Hypericum*, the flowers of which are very simple.

Still I think from my own experience, there can be no possible doubt either that the flower has modified the habits and structure of the insect, or that the insect has modified the habit and structure of the flower. Of the two, it seems to me, as a botanist, that the flower has been the predominant factor; but this opinion may be the result of prejudice.

Note.—Mr. G. H. Verrall, who has kindly looked through this paper, says that it is difficult to distinguish *Empis vitripennis* from about twenty closely allied species, several of which are yet unrecorded as British; that *Eristalis pertinax* has never been clearly differentiated in print, and that both *Syrphus cinctellus* and *S. ribesii* are very difficult to distinguish from numerous allied species.—H. G.